Chapter 5.2

Responses to Increased Moisture Stress and Extremes: Whole Plant Response to Drought under Climate Change

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Introduction

Drought is the most common abiotic stress reducing the yield of many crops, in particular legumes. Improving the tolerance of crops under water-limited environments is a must if agricultural production is to keep up with the expected demographic increase. Beyond productivity, resilience of crops to water limitation, i.e., the capacity to yield even under very harsh conditions, will be increasingly important with the ongoing and predicted changes in climate. All the Global Circulation Models (GCMs) predict that the current increases in temperature will continue so that by the end of the present century mean temperatures will be 2–4°C warmer than the present (Christensen et al. 2007). While the GCMs predict rainfall less reliably than temperature, the consensus is that the semiarid regions away from the equator will have decreasing rainfall and increasing periods of drought (Christensen et al. 2007; Hennessey et al. 2008). Again, while predictions of extreme events are less reliable, the consensus view is that supraoptimal temperatures and periods of drought and flooding rains will increase (Christensen et al. 2007; Hennessey et al. 2008), increasing the requirement for greater crop resilience. Finally, the change in temperature will also affect how crops grow and develop, even if water is sufficient, and this will have consequences on how crops respond when water becomes limiting. Thus, climate change will add a new dimension to the current research on drought and a comprehensive approach is needed to address drought in a way that takes into account how climate change will affect how plants use water and respond to drought.

In this chapter, we tackle the physiology of plant water use from the angle of how this will be modified in a context of a changing climate. Two recent reviews cover a number of innovative aspects to drought research, in particular in relation to research on roots, and advocate the need to look at the soil–root–shoot–atmosphere water management in a comprehensive and dynamic manner (Vadez et al. 2007, 2008). In the present chapter, we revisit some of these aspects from the perspective of changing climatic conditions and explore the major issues that climate change

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will bring about, and how it will affect crop production and in particular under water-limited conditions. These issues can be broadly grouped into two categories: (1) thermodynamic aspects of the soil–plant–atmosphere water relations and (2) growth and development aspects.

By "thermodynamic aspects of soil–plant–atmosphere water relations," we tackle the fact that temperature will increase, either the well-predicted 2–4°C increase or the increase in supraoptimal temperature events, and although the relative humidity may increase (Roderick et al. 2007), we may expect that the vapor pressure deficit (VPD) would increase because the magnitude of the relative humidity increase is expected to be less than the magnitude of the temperature increase. We will start this section by reflecting on the fact that drought effects are often consequences of differences in patterns of water use while water was available, and where we believe that plant hydraulics would play an important role. The increase in VPD will increase the rate of transpiration per unit leaf area and may have consequences on the hydraulic relations along the soil–plant–atmosphere continuum. Understanding the conductance to water of these different compartments will be an important aspect of selecting those genotypes that are better suited to climate change. This will need an improvement in the methods to assess the role of roots (Vadez et al. 2008) and require a thorough investigation of how genotypes control water loss at the leaf level and how this interacts with the increased VPD. We will also review the decreased water productivity due to the increase in VPD, and how understanding the processes of water loss at the leaf level are likely to be key to developing genotypes adapted to climate change.

By "growth and development processes," we mean all processes that will be influenced by temperature per se and by the rise in CO_2 concentration. First and foremost, the increase in temperature will increase the phenological development of the crop and shorten the cropping cycle. This will have an influence under all conditions, not only drought, and will simply represent a loss of opportunity to fix carbon and intercept light. The increase in VPD will likely have an effect on leaf expansion, which in consequence will affect both the crop biomass productivity and also the crop water balance under conditions of water deficit. We will address how shortening the cropping cycle, and increasing water demand because of VPD, may balance each other with limited consequences on the overall soil water balance. We will briefly address how the rise in CO_2 will have a beneficial effect on water productivity, which will in part counterbalance the negative effect of VPD increase on water productivity but not discuss the short- and long-term acclimation to higher CO_2, which is still the object of debate. We will address how breeders will have to select new cultivars with phenological development and overall strategies of water use that are suited to the changes in climate, in particular the ability to meet the demand for water at critical stages in crop development. In this section, we will also address how supraoptimal temperatures will have a dramatic effect on seed setting. This fact is well known and the challenge will be to identify genotypes capable of successful reproduction at high temperature.

Thermodynamic effects

How climate change will affect the control of plant water loss

Under conditions of climate change, temperatures are almost certain to increase and even if air humidity increases slightly, the VPD will likely increase. It is well known that the water moves along the soil–plant–atmosphere continuum driven by differences in water pressure. The increase in VPD will simply increase the difference between the wet leaf interior and dry atmosphere and tend to drive water out of the leaves and lead to more rapid depletion of the soil moisture profile unless the stomata close to reduce the water loss from the leaves. If plants can control water loss at high VPD when water is plentiful, this should make it more available when rainfall diminishes, a strategy that would be particularly

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important in conditions of terminal stress. So, our first line of action against climate change is to tackle the control of plant water loss under well-watered conditions. For that purpose, we need to understand better the hydraulic issues related to water movement in the soil–plant–atmosphere continuum.

The soil–plant–atmosphere continuum

Besides the fact that roots supply water to the plant and contribute to the overall plant water balance, relatively little is known about the processes and regulation of water uptake. It is well established that the hydrostatic pressure created by transpiration from the shoot is transmitted to the xylem vessels of the shoot and the roots, which drives water in the root cylinder toward the xylem vessels (Steudle 1995; Tyree 1997). It is also clear that the hydrostatic pressure is not the only factor responsible for water uptake, which also involves specialized membrane transporters (aquaporins) (Chrispeels and Maurel 1994; Javot and Maurel 2002; Tyerman et al. 2002; Bramley et al. 2007, 2009). The current model of water uptake through the root cylinder to the xylem, the composite transport model (Steudle 2000a), is such that water is taken up via three major pathways: (1) an apoplastic pathway where water travels through the apoplast of the cells in the root cortex, toward the endodermis and the xylem vessels, (2) a pathway of symplastic water transfer where water goes through cells traveling in the membrane continuum (endoplasmic reticulum and plasmodesmata) (cell-to-cell pathway), and (3) a pathway that involves water movement through the vacuoles and often merged to the symplastic pathway. The symplastic pathway usually is considered to offer a large resistance to water flow in contrast to the apoplastic pathway, which predominates when transpiration demand is high (Steudle 2000a, 2000b).

At constant leaf area, there are several possible ways by which plants can avoid losing excessive water even if water is available: (1) by having a lower stomatal conductance and (2) by limiting stomatal conductance when the VPD is high. We could also hypothesize that limiting root conductance to water entry would in turn induce stomatal closure under conditions of high evaporative demand. Some of these hypotheses are supported by a modeling study showing that imposing a maximum rate of transpiration per day would contribute to water saving, increase the transpiration efficiency (TE), and lead to a yield benefit in sorghum in most years (Sinclair et al. 2005). The challenge will be to identify genotypes that are capable of controlling water loss.

Understanding better the root hydraulic conductance to water

Under various stresses such as drought, salinity, waterlogging, nutrient deficiency, root aging, or environmental conditions such as temperature, humidity, or light, the resistance to water flow varies (Steudle and Henzler 1995; Bramley et al. 2010), and, for instance, usually increases under water deficit (Steudle 2000a). Most of that resistance is located in the root cylinder (radial resistance), whereas xylem vessels normally offer much less resistance (axial resistance) (Steudle 2000a; Bramley et al. 2009). In the root cylinder, the cell-to-cell pathway is a highly regulated movement, involving the crossing of many membranes through membrane transporters (aquaporins) (Javot and Maurel 2002; Tyerman et al. 2002; Bramley et al. 2007).

Understanding which components of the composite model (Steudle 2001) predominate under nonstressed conditions, and how these components change under water deficit, are crucial in understanding how plants regulate the rate of water and nutrient supply at the root level and eventually support transpiration and growth. Several reports have shown intra- and interspecific differences in the relative proportion of water traveling through each of these pathways (Steudle 1993; Steudle and Frensch 1996; Yadav et al. 1996; Steudle and Petersen 1998; Jackson et al. 2000; Bramley et al. 2009). Intraspecific differences in the hydraulic properties

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of roots would affect the rate of soil water use, or would lower the root length density (RLD) needed to absorb a given amount of water. So, under drought-prone conditions and moreover with climate change, the regulation of root hydraulic conductance is likely to be a key to the overall control of water loss by plants.

The need to approach roots "dynamically"

A better understanding of the dynamics of plant water use under both well-watered conditions and upon exposure to water deficits will be crucial to progress toward the identification of genotypes that can match water requirement and availability with climate change. Rooting traits will continue to be an important component in the overall plant adaptation to drought. However, it appears that there is a need to better understand root functionality rather than deciphering its morphology. Despite a substantial number of studies on roots in different crops, most of these studies assessed roots in a very "static" manner, i.e., destructive samplings at one or several points in time, giving virtually no information on the detailed "dynamics" of roots, and it is still unclear what particular root trait, or what particular aspect of root growth would contribute to a better adaptation to drought. In addition, most studies on roots published thus far have relied on a fundamental assumption, that increased RLD would equate with higher water uptake and therefore on yield.

As suggested by other authors (McIntyre et al. 1995; Dardanelli et al. 1997), water uptake should be the primary focus of root research and such water uptake should be assessed in vivo and repeatedly in plants that are adequately watered and are exposed to stress in conditions that mimic field conditions, particularly in relation to soil depths and soil volume per plant. In a previous review (Vadez et al. 2008), we have advocated that water uptake by roots should be measured rather than assessing morphological rooting traits. This methodological approach should be complemented by a comprehensive study on how roots and shoots capture and regulate water loss in a way that maximizes and matches plant productivity to available water.

VPD effect on water productivity

Water-use efficiency (WUE) can be defined at several levels: (1) at the cellular level as the ratio of instantaneous carbon fixation/instantaneous transpiration (A/E), (2) at the plant level as the ratio biomass/water transpired (also called TE), and (3) finally at the field level as the ratio of harvestable yield or above-ground biomass/evapotranspiration (also called WUE). Here, we will deal with TE, which is usually a major portion of WUE although soil evaporation can be a large fraction of evapotranspiration in some dryland situations.

As per the different definition of TE (reviewed by Tanner and Sinclair 1983), the productivity of water is an inverse relation of VPD, such as

$$Y/T = k(/e^* - e)$$ (Bierhuizen and Slatyer 1965),

where Y represents biomass or grain yield, T is transpiration, e is the vapor pressure in the atmosphere, and e^* is the saturated vapor pressure (the term $e^* - e$ represents VPD).

So, it appears from this definition that the water productivity of crop is constant except for a constant k that is crop specific. A recent review paper (Steduto et al. 2007) confirms these facts and also states that the only major differences in the k constant would be between C_4 and C_3 plants, whereas k would normally vary little within either C_3 or C_4 plants. However, they agree with a growing number of experimental data showing genotypic differences in TE in several crops such as groundnut. There is indeed a growing body of evidence showing that TE varies across genotypes of the same species, and then among species. Steduto et al. (2007) attribute the differences in TE with variation in the metabolic costs with respiration expenses differing among genotypes. So, for water-limited environments,

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whether water productivity can be improved toward better yields in specific environment/crops is still a major question mark. At ICRISAT, considerable effort is ongoing to develop groundnut genotypes with improved WUE. It has been shown in groundnut that higher TE leads to higher yield under intermittent stress conditions (Wright et al. 1991; Ratnakumar et al. 2009), but more work is needed in other legume crops.

The definition of TE by Bierhuizen and Slatyer (1965) simply indicates that if VPD increases, the water productivity will decrease at a constant rate. So, while the debate is still ongoing in relation to the constant k, i.e., the slope of the linear relationship between Y and T, no one has attempted to address whether the relationship between TE and VPD follows a similar decline in all genotypes. At ICRISAT, we have initiated some research on this by measuring TE in groundnut and pearl millet genotypes, where TE was measured at different VPD level ranging between 0.7 and 3.2 kPa using controlled environment growth chambers. Preliminary data indicate that not all genotypes have a same rate of decrease in TE upon increasing VPD (data not shown). For instance, TE in genotype ICGV86031, previously used as high TE parent in a crossing program (Krishnamurthy et al. 2007), had a higher TE than the low TE parent TAG24 under low VPD. However, the difference in TE between the genotypes was much less at higher VPD levels.

Regulation of stomatal control

A key to identifying germplasm with superior water productivity is a better understanding of the control of leaf water losses. Recent data in pearl millet (Kholova et al. 2010) and groundnut (Vadez et al. 2007; Bhatnagar-Mathur et al. 2008) report genotypic differences in the control of water loss under well-watered conditions, with important consequences on how genotypes respond later to a water deficit. Recent work on the *ERECTA* gene that controls TE shows that it has a role both in regulating photosynthesis and also in regulating stomatal conductance (Masle et al. 2005). ERECTA is a putative leucine-rich repeat receptor like kinase with known effect on the inflorescence development. This would potentially lead to a limit on the maximum rate of transpiration. Data on pearl millet and groundnut (Vadez et al. 2007; Bhatnagar-Mathur et al. 2008) indicate that genotypes better adapted to certain drought conditions might be those capable of limiting water use when water is available. In short, this type of behavior, i.e., water sparing by the shoot in the vegetative phase when the soil is wet, should make more water available for water uptake by roots at the grain-filling period. However, a more moderate water use in the vegetative stage will result in less photosynthetic activity and growth. While this water-sparing will be beneficial where crops grow on stored soil water, it can lead to lower yields where crops grow on current rainfall in a short rainy season (Turner and Nicolas 1998). What is usually called "drought tolerance" can at least in part be the consequence of constitutive traits that impact on how soil water is used when it is nonlimiting to plant transpiration.

Sensitivity of stomata to VPD to save water in the soil profile

Transpiration of certain genotypes of soybean has been shown to no longer increase or to increase at a lower rate at VPDs above 2.0 kPa (Sinclair et al. 2008). This trait would limit soil moisture use when the VPD is high, hence when carbon fixation has a high water cost. Similar and additional to the above trait, it would make more soil water available for grain filling. Certain species such as pearl millet in semiarid conditions have been reported to limit the increase in transpiration when the VPD is above 2.5 kPa (Squire 1979). In the work reviewed by Bidinger and Hash (2004), no attention was paid to possible genetic variations in this strategy. Our recent data indicate that a behavior similar to that in soybean is occurring in pearl millet, where genotypes differ in their transpiration response

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to VPD (Vadez et al. 2007b). Incorporation of a terminal drought tolerance Quantitative Trait Locus (QTL) considerably slowed transpiration at high VPD, whereas in genotypes not incorporating this QTL, the rate of transpiration responded linearly to increases in VPD above 2.0 kPa. We have also found similar results in groundnut, where transpiration responded linearly to an increase in VPD above 2.0 kPa in the genotype TAG24, whereas transpiration did not increase when the VPD was above 2.0 kPa in the genotype ICGV86031 (Devi et al., 2010).

Growth and development processes

Shortening of the cropping period

The phenological stages of plants are related to the accumulation of thermal degrees above a baseline temperature defined for each crop. Figure 5.2.1 shows the accumulation in degree-days in chickpea, using a base temperature of 8°C. It shows that a standard genotype requiring about 800 degree-days to reach flowering in the current climate would accumulate a similar number of degree-days in about 8 days less when the mean temperature increases 2°C. A warming climate has a similar effect on the time to maturity. Such a decrease in the overall cropping cycle is going to be one of the major effects of climate change. The consequences are twofold: (1) the shortening of the cropping cycle should, in theory, make the water requirement of the crop smaller and simulate the effects of short-duration cultivars, a breeding objective for water-limited environments and (2) the shortening of the cropping cycle represents a substantial decrease in the magnitude of light capture by the crop canopy and simulation modeling indicates that this will lead to a substantial yield decline in most situations and crops. To recover that loss in duration in cropping cycle, and the related decline in yield, the simplest solution will be to use slightly longer duration genotypes and cultivars than those currently being used.

Leaf expansion

Leaf expansion rate is normally linearly related to accumulation of thermal time in cereals. However, leaf expansion is affected by VPD and decreases under high VPD in maize (Reymond et al. 2003). A lower leaf expansion rate would then lead to lower leaf area. If climate change

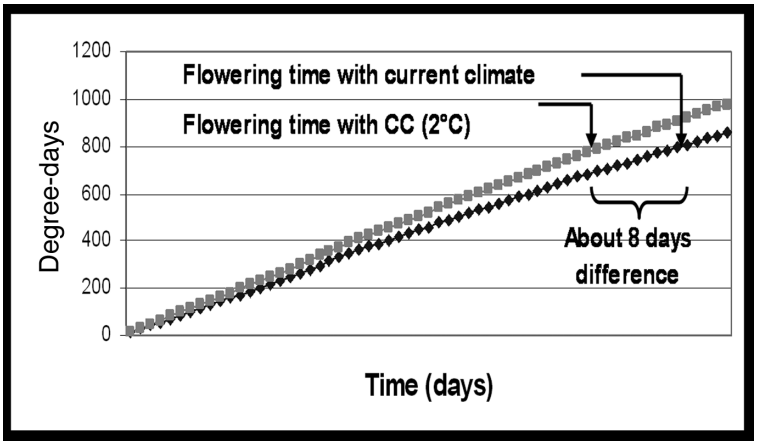

Fig. 5.2.1. Degree-day accumulation in chickpea using a base temperature of 8°C. It uses mean daily temperature data of the month of November and December 2008 at ICRISAT headquarters (Patancheru, Andhra Pradesh). The climate change (CC) scenario is using an increase of 2°C above current climate.

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results in higher VPDs, we can expect that the leaf canopy will develop differently as a result of climate change and may differ among species and genotypes. While leaf expansion in crops, such as maize, takes place primarily during the night; in pearl millet, leaf expansion takes place during both day and night. This is an important issue as minimum temperatures have been shown to increase more than maximum temperatures and maximum relative humidities to decrease as a result of global warming. Therefore, an expected effect of climate change on the leaf area development may have different effects on different species, depending whether leaf expansion takes place predominantly during the night or the day in these species. Preliminary data at ICRISAT indicate that groundnut genotypes vary in leaf area development under different VPD conditions. The genotype TAG24 showed almost no decrease in leaf area at moderate VPD, whereas genotype ICGV86031 showed a significant decrease in leaf area. On the one hand, a decrease in leaf area will limit productivity and will limit carbon fixation, while a smaller canopy will limit water extraction from the soil profile, which should be beneficial for crops growing on stored soil moisture.

Length of the growing period (LGP)

This parameter is defined as the number of days during a cropping cycle when there is sufficient water in the soil profile to sustain growth. With the increase in temperature, the evaporative demand is likely to increase, although because of the influence of the increase in temperature on leaf area and growth, the increase may not be as great as expected from the changes in VPD. Simulations and modeling indicate that the LGP will likely be shortened under climate change conditions by up to 20% in some African regions (Thornton et al. 2006), in part because of the delay in reliable opening rains (Tadross et al. 2007). How the reduction in the cropping cycle will in part compensate for the reduction in the LGP is an important question if we are to answer issues arising from climate change. We will attempt to do so in the following section, looking it from the angle of the overall plant water management.

The compensating effect of CO_2

High intrinsic WUE, i.e., the ratio of photosynthetic and transpiration rates at the leaf level, is achieved by having a low CO_2 concentration in the substomatal chamber (Condon et al. 2002). A high mesophyll efficiency would contribute to that by driving the CO_2 concentration down in the substomatal chamber. It can also be achieved by maintaining a low stomatal conductance. Increasing CO_2 concentrations in the atmosphere will reduce stomatal conductance, but plants should be able to maintain similar CO_2 concentrations in the substomatal chamber with a lower stomatal conductance, which will result in lower rates of transpiration and this will contribute to water saving. Therefore, we can expect that the higher CO_2 conditions brought about by climate change will have a beneficial effect on the overall plant water balance and productivity, as it has been show previously (Sinclair et al. 1991). The fact that the stomatal conductance would be less in a higher CO_2 environment would also relieve plant hydraulics with regards to water movement. Obviously, the reduced transpiration and related reduction in leaf cooling will have to be considered from the angle of possible heat stress on the leaves.

Matching water uptake to the overall cropping cycle—plant phenology

The shortening of the cropping period and the quicker water exploitation from the soil profile due to higher VPD and the temperature-related differences in the canopy development will have antagonistic effects on the overall water balance of the soil profile. From a water-availability point of view, the strategy to identify successful genotypes fitted to the water-limited conditions under the climate change scenario will need to be based on the following two basic requirements:

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(1) to maximize transpiration and water capture and (2) to ensure that water is available for key stages in crop development and in particular in the postflowering period.

Under drought conditions, the primary factor contributing to better yield is suitable phenology, adjusted to the water available from rainfall or soil moisture to allow the crop to complete its life cycle (drought escape mechanism) (Serraj et al. 2004). Several studies indicate that "superior" root traits contribute to drought tolerance of genotypes, provided these have a suitable phenology (Blum et al. 1977; Kashiwagi et al. 2006). Therefore, while measuring the volume of water taken up by roots is certainly an important factor, understanding the kinetics of water uptake, and how these kinetics relate to the phenological stage of a plant, are equally important issues. This view is shared by Boote et al. (1982, cited in Meisner and Ketring 1992), who argue that sufficient amounts of water at key times during the plant cycle is more important than availability across the whole cycle. We suggest that these key stages may be the reproductive stages and the later stages are the grain filling. Previous work on roots indicates that root growth can persist at very different stages and under different conditions, such as drought (Chopart 1983; Hafner 1993; Ketring and Reid 1993). However, a missing link in these studies is how the reported root growth relates to differences in water uptake, and how much the water uptake varies among genotypes over the growth cycle. Therefore, our working hypothesis is that differences in root growth under drought during reproduction and the latest part of grain filling will result in differences in water uptake, in turn resulting in differences in seed number and better grain filling.

One exception to this emphasis on reproductive growth being critical is the prediction that climate change will reduce the probability of rainfall at the beginning of the growing season in southern Africa, thereby shortening the length of the growing season (Tadross et al. 2007). If genotypes of crops that can withstand early drought could be developed, this would enable them to be sown on limited rainfall and earlier than waiting for good opening rains. Studies with wheat, lupins, and faba bean suggest that provided there is sufficient rain for germination and emergence, the seedlings can withstand periods of up to a month without follow-up rainfall. Screening for differences in seedling survival without water would be an easy and effective solution for such a drought/climate change scenario.

Water uptake during reproduction

The reproductive stages of crop plants are extremely sensitive to any type of stress (Boyer and Westgate 2004). First, we consider the reproductive stages as the sequence of events from the emergence of a flower bud to the beginning of grain filling. It is important to understand the kinetics of water supply under stress during these stages, the existence of any genotypic difference in the kinetics, and how such differences relate to yield. Our data (Vadez et al. 2008) showed that groundnut genotypes grown in 1.2 m and 16 cm diameter PVC cylinders and exposed to water stress during flowering had very distinct patterns of water use. Genotypes TMV2 and ICGS 44 maximized transpiration during the first 10 days following withdrawal of irrigation, but ran short of water during later stages. By contrast, genotypes TAG 24 and ICGV 86031 limited their transpiration soon after withdrawing irrigation, but were able to extract water for a longer period of time. We found that genotypes TAG 24 and ICGV 86031 had higher abscisic acid (ABA) content in the leaves under stress conditions than under well-watered conditions, whereas TMV2 and ICGS 44 had similar ABA levels under both treatments (Fig. 5.2.2). Genotypes TAG 24 and ICGV 86031 had higher ABA content under stress conditions than TMV2 and ICGS 44 under stress conditions. We did not test whether these differences in kinetics had any bearing on the relative yield. However, the data clearly suggested that genotypes differed in their kinetics of water uptake under stress. What consequences this

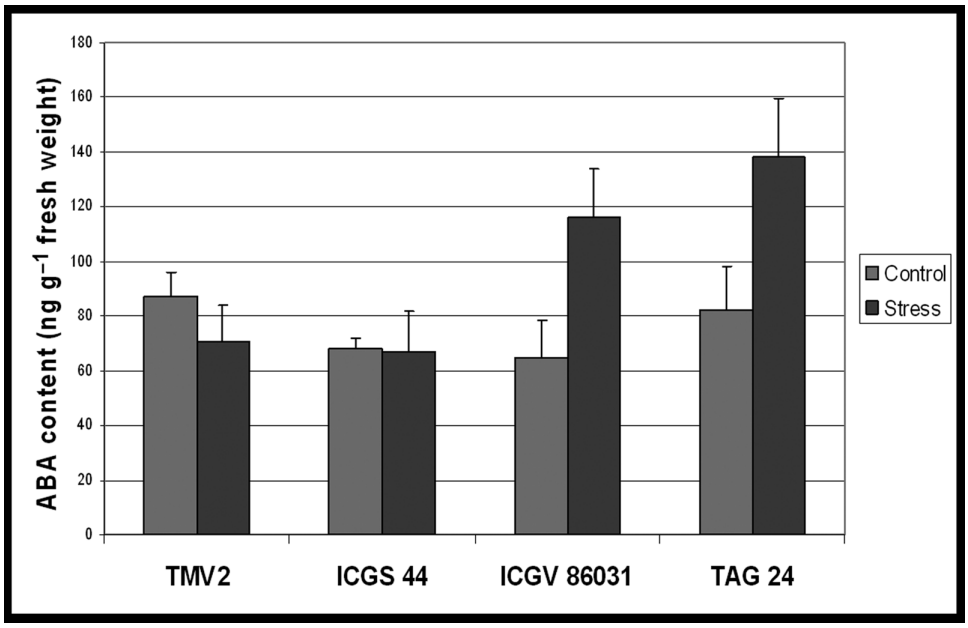

Fig. 5.2.2. ABA content (ng g^{-1} fresh weight) in the leaves of four groundnut genotypes grown in 16 cm PVC tubes and either grown under fully irrigated conditions (control) or under water stress conditions (stress), which was imposed by withholding irrigation from 40 days after sowing. Leaf tissues were sampled at 24 days after withdrawing irrigation.

had on reproduction still needs to be elucidated. The data also suggest that ABA is likely to play a role in the kinetics of water uptake.

Water uptake and grain filling

Differences in water uptake during grain filling will also affect photosynthesis and consequently the supply of carbohydrates to the maturing grains. For instance, a good relationship between RLD in the deep soil layers and the harvest index (indicative of grain filling) was observed in chickpea, especially under severe drought conditions (Kashiwagi et al. 2006). A similar phenomenon may also prevail in sorghum where the stay-green phenotype is associated with better grain filling, and where one hypothesis is that the maintenance of physiologically active and green leaves under terminal moisture stress, along with a minimum water uptake, sustains grain filling under terminal drought. This is in agreement with the observed deeper rooting of stay-green genotypes under water-stressed conditions (Vadez et al. 2005, 2007a). The water needed to sustain grain filling may be relatively small and due to small differences in root development (depth, RLD). Such differences would be difficult to capture by current measurements of root growth (biomass, RLD, root length), but could be measured by an assessment of water uptake, which would "integrate" the benefit of slight RLD differences over time.

The effect of high temperature on pod setting

Climate change is expected to raise the frequency of extremes of cold and heat in different parts of the world (Christensen et al. 2007; Hennessey et al. 2008). Yet, heat waves are a common characteristic of the semiarid tropics and developing cultivars to withstand supraoptimal temperatures

is important. It is well known that plant's reproduction is sensitive to heat stress (Prasad et al. 2000, 2001, 2002, 2003, 2006a, 2006b). Therefore, it will be important to identify genotypes that are capable of setting seeds at supraoptimal temperatures. In doing so, care should be taken with the experimental approach as simply delaying the date of planting to ensure that reproductive development occurs at high temperatures will also affect the radiation received by the crop. To reliably screen for the ability to set seed at high temperatures, controlled environment conditions will be required.

Crop failure

One of the consequences of increasing temperatures and increasing frequency of drought is the increase in crop failure. Modeling suggests that where crop production in currently marginal climate change will result in a greater number of years when crops fail (Thornton et al. 2006). While one or two years of crop failure may be manageable in the developed world, for subsistence farmers, it can result in abandonment of the farm. The switch to livestock production and reliance on perennial grasses and shrubs for fodder may be required for survival in areas marginal for cropping.

Conclusion

As can be seen, climate change will induce a number of changes that will affect the evaporative environment in which plant leaves will evolve. A better understanding of the process by which plants control their water loss is needed, in particular to achieve a tighter control. A better understanding of the hydraulic relations along the soil–plant–atmosphere continuum is required. Regarding the role of roots, it will become increasingly important to address rooting traits in a more dynamic manner, in particular looking in a comprehensive manner at how a particular pattern of water uptake will match the control of water loss by the leaves. Since water productivity will decrease as the climate changes due to an increase in the VPD, the challenge will be to identify germplasm that is capable of maintaining high water productivity under high evaporative demand.

Climate change will also affect the overall pattern of the cropping cycle. Breeding for medium duration crops will likely be increasingly important and this should largely mitigate the negative effects of climate change on yield. With increasing likelihood of drought, a key will be to understand the dynamics of water uptake and how water taken up at key developmental stages affects the yield under stress.

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